



Evolution of Land Plants

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Introduction

The colonization of land by plants was one of the most important events in the earth's history, setting the stage for the greening of the continents, increased oxygenation of the atmosphere, and the provision of food and habitat for the animals and microorganisms that evolved in parallel—and in many cases, diversified in their shadows. They are the foundation of agriculture and the source of timber, fibers, pharmaceuticals, and psychoactives. Fossilized plants, in particular, drive our global economy, being the source of coal, petroleum, and natural gas. And living plants represent huge above- and below-ground (as roots and microalgae) carbon sinks. Continental colonists who appeared before land plants (embryophytes) included prokaryotic microbes, eukaryotic microalgae, and fungi. The conditions necessary for colonization—sufficient areas of stable land accessible to marine and aquatic organisms, formation of soils, and equable atmospheric and climatic conditions—appear to have been established approximately 540–440 million years ago (MA; Cambrian and Ordovician). By about 470–460 MA (middle Ordovician), plant microfossils first appear in the fossil record, including spores, cuticular fragments, and tracheid cells. Early plant micro- and macrofossils, when considered together, displayed adaptations that facilitated survival on land, including coatings to reduce desiccation, stomata to facilitate gas exchange (in all lineages but liverworts), and specialized cells such as tracheids for the movement of water and nutrients (precursors of a vascular system). By about 410 MA (late Silurian to early Devonian), vegetation comprising small plants with a well-developed vascular system was establishing itself on multiple continents. From about 390–360 MA (middle to late Devonian), the number of species increased rapidly, and by 360 MA the major extant lineages of land plants were established. Major innovations in plant form began to appear, including the capacity to attain great height and size, and in the late Devonian period, the evolution of seeds. The seed provided protection during periods of dormancy and facilitated survival at greater distances from water. These events were followed during the Cretaceous/Cenozoic by one of the most spectacular radiations of any terrestrial clade: the rise of the angiosperms, which in the 21st century constitute about 90 percent of all land plant diversity.

General Overview

Today's flora has been assembled from just ten major living lineages or clades (a branch in the phylogeny that includes an ancestor and all its descendants). These are: three clades of non-vascular plants (liverworts, mosses, and hornworts [collectively, the bryophytes]); and seven clades of vascular plants, two of which are free-sporing, or lacking in seeds (lycophytes and ferns); and five of which are seed-bearing (cycads, ginkgo, conifers, gnetophytes [collectively, gymnosperms], and angiosperms). Diversification into all of these clades except the angiosperms had occurred by about 360 MA (Bell and Hemsley 2000). Gymnosperms in particular were previously much more numerous; up to 70 percent of their major lineages became extinct after the origin of angiosperms (Friis, et al. 1987). All land plants share the characteristic that they produce two distinct multicellular structures, a haploid gamete-bearing plant (gametophyte) and a diploid spore-bearing plant (sporophyte). Multicellular gametophytes are shared with their algal relatives, but multicellular sporophytes are a hallmark of land plants. The earliest land plants were relatively simple in form, and paleo- and neobotanical evidence suggests that they resembled mosslike plants (Willis and McElwain 2014). Cellular differentiation of both vegetative and reproductive structures was limited, and they lacked leaves, roots, and seeds. Their size was restricted by the lack of strengthening tissue and a vascular system to conduct water and nutrients. Living members of the earliest diverging lineages of land plants (bryophytes) mostly retain this simplicity and small size. A key feature of bryophytes is the predominance of the gametophytic stage of the life cycle and the dependence of the smaller, more ephemeral sporophytes on the gametophyte. In vascular plants (tracheophytes), on the other hand, branched sporophytes live independently from the much smaller and often ephemeral gametophytes. This evolutionary progression from a dominant haploid phase in the earliest land plants to a dominant diploid phase in vascular plants is a key theme of land plant evolution (Kenrick 2017). The origin of sporophytic dominance has been explained by two debated hypotheses: the homologous and the antithetic (or intercalary) hypotheses (Kenrick and Crane 1997). The first proposes that the ancestral sporophyte and gametophyte were morphologically similar and have since diverged. The second invokes the novel origin of a multicellular sporophyte that resulted from a delay of meiosis coupled with mitotic divisions in the zygote, producing an embryonic sporophyte retained by, and dependent on, the larger gametophyte. The following sections list key texts or focus on the evolution, diversity, and global impacts of land plants.

Bell, Peter R., and Alan R. Hemsley. 2000. *Green plants. Their origin and diversity*. 2d ed. Cambridge, UK: Cambridge Univ. Press.

A broad survey of the diversity of both living and extinct plant taxa.

Friis, Else M., William G. Chaloner, and Peter R. Crane, eds. 1987. *The origins of angiosperms and their biological consequences*. New York: Cambridge Univ. Press.

A collection of chapters focusing on the origin of angiosperms and changes in the earth's flora and fauna during the development of angiosperm-dominated plant communities.

Kenrick, Paul. 2017. Changing expressions: A hypothesis for the origin of the vascular plant life cycle. *Philosophical Transactions of the Royal Society of London B* 373:20170149.

An important article that synthesizes evidence from fossils of the Rhynie chert with advances in developmental genetics and plant phylogenetics, focusing on different hypotheses explaining the free-living sporophyte of vascular plants and highlighting the importance of this transition in the subsequent evolution of land plants.

Kenrick, Paul., and Peter R. Crane. 1997. *The origin and early diversification of land plants: A cladistic study*. Washington, DC: Smithsonian Institution Press.

An exceptional and comprehensive study of mostly macrofossil evidence on origins and early diversification of land plants. Also discusses historical theories on the origin of land plants. It is a valuable source of information on both living and extinct plants, and on their traits and evolution. Data were amassed from macrofossils and living plants for cladistic analyses to clarify relationships among major groups of land plants except seed plants.

Willis, Katherine J., and Jennifer C. McElwain. 2014. *The evolution of plants*. Oxford: Oxford Univ. Press.

A broad survey of the diversity of both living and extinct plant taxa with a phylogenetic focus.

Books

The introductory texts below provide a broad perspective on topics ranging from the palaeobotanical record of land plants, the transition to life on land, the diversity of extinct and extant plant groups, and ecological associations. Bold, et al. 1987 and Gifford and Foster 1988 provide detailed coverage of the morphology and diversity of green plants and vascular plants, respectively. Bell 2008; Judd, et al. 2008; and Friis, et al. 2011 focus on the morphology, paleobotany, and phylogenetics of flowering plants. Raven, et al. 2013 is a widely used text that is updated regularly. Niklas 1997 uniquely synthesizes aspects of land plant evolution that include morphology, biomechanics, phylogenetics, and microevolutionary processes. Stewart and Rothwell 1993 and Taylor, et al. 2009 are key paleobotanical texts.

Bell, Adrian D. 2008. *Plant form. An illustrated guide to flowering plant morphology*. Portland, OR: Timber Press.

A detailed glossary on anatomy, architecture, and morphology of angiosperms. Illustrated with hundreds of line drawings and color photographs highlighting key features from relevant taxonomic groups.

Bold, Harold C., Constantine J. Alexopoulos, and Theodore Delevoryas. 1987. *Morphology of plants and fungi*. 5th ed. New York: HarperCollins.

A classic text that covers morphological variation and life cycles of major land plant clades.

Friis, Else M., Peter R. Crane, and Kaj R. Pedersen. 2011. *Early evolution of flowers and angiosperm evolution*. Cambridge, UK: Cambridge Univ. Press.

Provides a synthetic perspective on the evolution of flowering plants that incorporates recent findings from paleobotany, phylogenetics, ecology, and geology.

Gifford, Ernest M., and Adriance S. Foster. 1988. *Morphology and evolution of vascular plants*. 3d ed. New York: W. H. Freeman.

An indispensable reference that covers morphological variation and life cycles of major vascular plant clades.

Judd, Walter S., Christopher S. Campbell, Elizabeth A. Kellogg, Peter F. Stevens, and Michael J. Donoghue. 2008. *Plant systematics. A phylogenetic approach*. 3d ed. Sunderland, UK: Sinauer.

A textbook that includes descriptions of major families of vascular plants (especially flowering plants) with detailed line drawings, presented in a phylogenetic context, and chapters on the evolution of plant diversity and green plant phylogeny. Also include synopses to numerous key topics in the field of plant systematics.

Niklas, Karl J. 1997. *The evolutionary biology of plants*. Chicago: Chicago Univ. Press.

A masterful work on the evolution of plants that includes chapters on the origins of adaptive traits that facilitated land plant evolution and the processes that underlie diversification.

Raven, Peter H., Ray F. Evert, and Susan E. Eichorn. 2013. *Biology of plants*. 8th ed. New York: W. H. Freeman.

A definitive introductory botany textbook covering the diversity of living land plants from a variety of perspectives, including evolution, ecology, morphology, anatomy, physiology, genetics, and conservation.

Stewart, Wilson N., and Gar W. Rothwell. 1993. *Paleobotany and the evolution of plants*. New York: Cambridge Univ. Press.

A seminal work on the palaeobotanical record of land plants. Like Taylor, et al. 2009, it includes chapters on the formation of fossils, life in the Precambrian, diversity of organisms other than plants, and terrestrialization of plants, with the core of the text being organized around the major groups of land plants. Generously illustrated.

Taylor, Thomas N., Edith L. Taylor, and Michael Krings. 2009. *Paleobotany. The biology and evolution of fossil plants*. 2d ed. Amsterdam: Academic Press.

A companion to Stewart and Rothwell 1993, covering related topics. This work, however, is considerably longer, due in part to detailed coverage of individual taxa. It additionally includes chapters devoted to plant morphology and anatomy and to plant-animal interactions. Lavishly illustrated, including numerous color plates.

Origin of Land Plants

Data from fossils, morphology, development, biochemistry, and molecular phylogenetics provide complementary insights into the nature of the earliest land plants and their shared ancestry with close algal relatives. Recent studies of plant structure and development suggest that embryophytes were derived from within the charophyte, rather than the chlorophyte green algae (Delwiche and Cooper 2015). The former includes important marine phytoplankton and the genetic model for green algae, *Chlamydomonas reinhardtii*. The charophytes are mostly freshwater organisms and display considerable morphological diversity. The first published phylogeny inferred from DNA sequence data (Karol, et al. 2001) confirmed that embryophytes were derived from within charophytes, and Niklas and Kutschner 2010 reviews the developmental and morphological evidence that links reproductive structures of charophytes and land plants. The question, nevertheless, of which of the six charophyte families is the closest relative has remained controversial, even with the advent of genomic data (Zhong, et al. 2015). Fossil evidence suggests the first land

plants were diminutive and without vasculature but were diverse in the structures of their spores and spore-bearing organs. The earliest evidence of fossilized remains that possess affinities to modern bryophytes, especially liverworts, are the cryptospores (Edwards, et al. 2014). Cryptospores are microfossils representing extinct lineages thought to include the progenitors of bryophytes, although this remains contentious. Their spores dispersed in groups of two or four, and they were abundant and widespread during the Ordovician thru the Devonian. Among the oldest unequivocal land plant macrofossils with affinities to vascular plants are the cooksonioids, including most famously *Cooksonia*, but also *Fusitheca*, *Salopella*, *Tarrantia*, *Tortilicaulis*, and *Uskiella* (Lang 1937, Edwards and Kenrick 2015, Boyce 2008). *Cooksonia* was about the same height of a matchstick and had leafless, branching sporophytes with stomata and a poorly developed vascular system composed of tracheids. Their sporangia were borne terminally on branches, and contained small spores with robust walls, likely an adaptation for wind dispersal potentially in harsh, dry environments. These resistant, sporopollenin-walled spores were often borne in tetrads, leaving characteristic trilete scars on the sporangia. This combination of features provides the best direct evidence for the earliest existence of land plants. More generally, the co-existence of sporopollenin-walled spores, waxy plant cuticles composed of cutan, and lignin in water conducting cells indicates indisputable evidence of plant life on land (Graham 1993).

Boyce, C. Kevin. 2008. How green was *Cooksonia*? The importance of size in understanding the early evolution of physiology in the vascular plant lineage. *Paleobiology* 34:179–194.

A review of early cooksonioid fossils, and a broad assessment of their morphology and physiology to assess the evolution of sporophytic independence among early vascular plants. The author argues that at least some early, smaller cooksonioid sporophytes were largely physiologically dependent on the gametophytes and not photosynthetically independent.

Delwiche, Charles F., and Endymion D. Cooper. 2015. The evolutionary origin of a terrestrial flora. *Current Biology* 25:R899–R910.

A careful review of fifteen years of relevant studies from DNA sequence data together with assessments from morphological and developmental evidence. It also makes sense of the substantial diversity of green algae and succinctly explains the different names that have been used for charophyte lineages.

Edwards, Diane, Jennifer L. Morris, John B. Richardson, and Paul Kenrick. 2014. Cryptospores and cryptophytes reveal hidden diversity in early land plant floras. *New Phytologist* 202:50–78.

A recent, detailed, review and synthesis of the early land plants from microfossils. These early pioneers were minute and lacked a vascular system but collectively harbored unexpected diversity in reproductive development as well as some surprising vegetative features. They also argue that early land plants represent an extinct pool of diversity from which both vascular and modern non-vascular plants (hornworts, liverworts, and mosses) were derived.

Edwards, Diane, and Paul Kenrick. 2015. The early evolution of land plants, from fossils to genomics: A commentary on Lang (1937) 'On the plant-remains from the Downtonian of England and Wales.' *Philosophical Transactions of the Royal Society B* 370:20140343.

A characterization and historical account of early land plant fossil discoveries and trait evolution aligned with modern interpretations of these fossils. Also integrates a comparative genomics perspective surrounding efforts to elucidate the evolution of stomata, cuticle, and vascular systems.

Graham, Linda E. 1993. *Origin of land plants*. New York: John Wiley.

A focused discussion on the origin of plants largely from the perspective of modern plants, with references to the paleobotanical literature relevant to early plant evolution. Integrates insights from paleontology, biochemistry, electron and fluorescence microscopy, and phylogenetics.

Karol, Kenneth G., Richard M. McCourt, Matthew T. Cimino, and Charles F. Delwiche. 2001. The closest living relatives of land plants. *Science* 294:2351–2353.

The first, broad four-gene phylogeny to clarify the relationships of land plants with their closest algal sisters. It was the first study to identify land plants as derived within Charophyta algae.

Lang, William H. 1937. On the plant-remains from the Downtonian of England and Wales. *Philosophical Transactions of the Royal Society of London. Series B* 227:245–291.

Pioneering research that led to the discovery and characterization of what are considered the earliest plants possessing a vascular system for conducting water and nutrients. More time and additional data on cryptic microfossils by Lang and others were required to understand the earliest land plant floras, comprising minute plants lacking vascular tissue.

Niklas, Karl, and Ulrich Kutschner. 2010. The evolution of the land plant life cycle. *New Phytologist* 185:27–41.

A notable review on the evolution of the land plant life cycle. Argues that reproductive organs of embryophytes are homologous with the multicellular gametangia of certain charophytes, which implies that these taxa are candidates for the closest relatives of embryophytes.

Zhong, Bojian, Linhua Sun, and David Penny. 2015. The origin of land plants: A phylogenomic perspective. *Evolutionary Bioinformatics Online* 11:137–141.

A succinct review focusing on phylogenomic investigations of the closest living relatives of land plants. It includes a useful discussion of the issues associated with analysis of data sets comprising sequence data from many concatenated genes.

Innovations That Facilitated Colonization

Several key features allowed plants to colonize terrestrial habitats. Comparative studies, including analyses of sequenced genomes (Hori, et al. 2014; Harholt, et al. 2016; Nishiyama, et al. 2018), reveal that some of these were shared by their closest algal relatives (the presence of a cell wall and the ability to direct the plane of cell division, coordination of cell and plastid division, evolution of the phenylpropanoid pathway that later facilitated the production of diverse secondary metabolites that function in protection from UV light and desiccation), while others likely evolved in the ancestor of land plants (alteration between multicellular haploid and diploid stages, evolution of water transport mechanisms; Rensing 2018). Initially, relatively simple water transport mechanisms were sufficient, due to high levels of atmospheric CO₂ during the colonization phase (Silurian-Devonian), which reduced the level of water flow through the plant that was required to acquire CO₂ for photosynthesis. By the end of the Carboniferous, as photosynthetic organisms withdrew atmospheric CO₂ to much lower levels, more elegant transport mechanisms evolved (Strullu-Derrien, et al. 2013). During the early Silurian, specialized cells containing lignin arose. These were programmed for early cell death, resulting in hollow tubes that formed a robust plumbing system, facilitating long distance water transport and much higher CO₂ diffusion rates for photosynthesis. These single cell conduits were composed of tracheids, a feature that unites all tracheophytes. The evolution of tracheids from more simple hydroids (found in many bryophytes) may have occurred more than once. The impregnations of spore walls with sporopollenin and the covering of plant surfaces with waxy cutin helped them avoid desiccation but also increased the need for more dynamic regulation of water transport. Stomata introduced internal controls on water movement (Sussmilch, et al. 2017) and likely evolved before tracheids, based on their presence in bryophytes. The evolution of water transport mechanisms and waterproof cuticles allowed plants to survive without being immersed in water. Additionally, during this time, an endodermis likely evolved. This important root structure sheaths the water conducting tissues and regulates ion exchange and microbial interactions between the conducting and outer root tissues. It can also help pressurize the water column and facilitate water movement. These innovations together enabled land plants to extract water directly from a soil matrix via their roots, and, ironically, their ability to survive extreme desiccation decreased. Finally, mutualistic and symbiotic microbes aided the establishment of plants on land by helping them cope with thin, nutrient-poor soils, and by increasing the water uptake by plant roots (Field, et al. 2015; Knack, et al. 2015).

Field, Katie J., Silvia Pressel, Jeffrey G. Duckett, William R. Rimington, and Martin Bidartondo. 2015. Symbiotic options for the conquest of land. *Trends in Ecology and Evolution* 30:477–486.

Outlines a series of outstanding questions regarding plant-fungal symbioses and the origin of land plants.

Harholt, Jesper, Øjvind Moestrup, and Peter Ulvskov. 2016. Why plants were terrestrial from the beginning. *Trends in Plant Science* 21:96–101.

Presents the idea that because incremental changes coinciding with land plant origins began to occur early in the evolution of charophyte algae, it would not be surprising to discover that diverse charophytes may have been experimenting with colonization, including representatives of lineages other than those that are most closely related to embryophytes.

Hori, Koichi, Fumito Maruyama, Takatomo Fujisawa, et al. 2014. *Klebsormidium flaccidum* genome reveals primary factors for plant terrestrial adaptation. *Nature Communications* 5:3978.

Presents insights from comparison of the whole genome sequence for the sister genus of the rest of the streptophytes with genomes of other plants and green algae and presents evidence that aspects of plant hormonal pathways are shared across land plants and algae. In addition, the study identifies protein encoding genes likely responsible for protection against high intensity light, indicating that algae evolved genetic mechanisms for life on land.

Knack, Jennifer J., Lee. W. Wilcox, Pierre-Marc. Delaux, et al. 2015. Microbiomes of streptophyte algae and bryophytes suggest that a functional suite of microbiota fostered plant colonisation of land. *International Journal of Plant Sciences* 176:405–420.

Presents findings from a metagenomics study indicating that modern streptophyte algae and bryophytes are associated with a diverse array of microbes involved in nitrogen fixation, methane oxidation, and B₁₂ synthesis.

Nishiyama, Tomoaki, Hidetoshi Sakayama, Jan de Vries, et al. 2018. The *Chara* genome: Secondary complexity and implications for plant terrestrialization. *Cell* 174:448–464.

In-depth analyses of the genome of *Chara braunii*. Reveals that features previously associated only with land plants evolved in the common ancestor of land plants and the charophyte lineages with which they share a phragmoplast, which orients the plane of cell division.

Rensing, Stefan. 2018. Great moments in evolution: The conquest of land by plants. *Current Opinion in Plant Biology* 42:49–54.

Summary of recent advances in our understanding of land plant colonization.

Strullu-Derrien, Christine, Paul Kenrick, Eric Badel, Hervé Cochard, and Paul Tafforeau. 2013. An overview of the hydraulic systems in early land plants. *International Association of Wood Anatomists Journal* 34:333–351.

Overviews fossil evidence of early tracheids suggesting that wood evolved in small stature plants before the evolution of distinct organs. Discusses the challenges and emerging approaches relating to the modeling of hydraulic function from morphology.

Sussmilch, Frances C., Timothy J. Brodribb, and Scott A. M. McAdam. 2017. What are the evolutionary origins of responses to abscisic acid in land plants? *Journal of Integrative Plant Biology* 59:240–260.

Covers the debate over two models to explain the evolution of the ability of plants to actively close their stomata in response to water deficit in leaves and presents evidence favoring a gradualistic model in which stomata of early vascular plants responded passively to water deficit.

Tomescu, Alexandru M. F., Sarah E. Wyatt, Mitsuyasu Hasebe, and Gar W. Rothwell. 2014. Early evolution of the vascular plant body plan—the missing mechanisms. *Current Opinions in Plant Biology* 17:126–136.

Detailed investigation on the origin of the branched sporophyte, arguably one of the most important early features in vascular plant evolution. Synthesizes morphology, developmental transitions, and genomics.

Insights from Phylogenomics

The development of phylogenetic methods, from cladistics to explicitly model-based likelihood and Bayesian methods, led to major advances in our understanding of land plant origins, colonization, and the tempo and mode of diversification. Early multilocus studies often sought to limit the number of loci sampled in order to include more taxa, but more recent efforts have capitalized on advances in whole genome sequencing to include hundreds of genes. Today, plant phylogenetic biologists routinely sequence whole genomes or large sets of loci (hundreds to thousands) to infer

phylogenetic relationships and patterns of genome evolution. Although phylogenetic results have in many cases supported earlier, morphology-based classifications, many surprises have emerged (Palmer, et al. 2004), including the potential non-monophyly of bryophytes; the monophyly of horsetails and ferns; the placement of gnetophytes, once thought to be sister to angiosperms, within or sister to extant conifers; and the sister group relationship of *Amborella* to all other angiosperms. Numerous advances in these areas have been translated to greatly revised classifications for a number of the largest land plant clades, including bryophytes, ferns, and angiosperms (e.g., Angiosperm Phylogeny Group 2016). Several relationships remain uncertain, however, including the relationships of charophyte lineages to land plants, and the branching order among modern bryophytes (Puttick, et al. 2018; Wickett, et al. 2014), which are crucial to understanding the evolution of early land plants and of vascular plants. Other results that remain controversial are the monophyly of extant gymnosperms, the early branching order of ferns and their allies, and the placement of *Amborella* on its own branch in the angiosperm phylogeny or in a clade with water lilies. Perhaps the single most important reference for assessing information on the phylogeny, taxonomy, and diversity of vascular plants is Angiosperm Phylogeny. This website is rigorously edited and regularly updated to reflect findings in the recent literature. Phylogenomic analyses also have confirmed the prevalence of whole genome duplication in flowering plants, revealed its occurrence in other seed plants, and provided evidence corroborating the hypothesis that following a genome duplication there is a delay in the realization of the evolutionary consequences of the duplication (Clark and Donoghue 2017; Estep, et al. 2014; Panchy, et al. 2016; Sharborough, et al. 2017; Cai, et al. 2019).

Angiosperm Phylogeny.

A comprehensive, frequently updated guide to the phylogenetic relationships of seed plants with associated classification, mostly at the level of orders and families. Includes descriptions of morphology, diversity, diversification, divergence time estimations, aspects of morphology, and ecology.

Angiosperm Phylogeny Group. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181:1–20.

A phylogenetic classification for the major families and orders of flowering plants.

Cai, Liming, Zhenxiang Xi, André A. Amorim, et al. 2019. Widespread ancient whole-genome duplications in Malpighiales coincide with Eocene global climatic upheaval. *New Phytologist* 221:565–576.

Applies transcriptome assemblies to conservatively infer the positions of 22 mostly previously undetected whole genome duplications in the evolution of the largely tropical angiosperm clade Malpighiales. These genome duplications cluster during the Eocene Thermal Maxima which marked the warmest and wettest period of the past 65 MYR. These results suggest a previously unrecognized period of prolific WGDs in land plants, which may have facilitated survival during dramatic periods of global change.

Clark, James W., and Philip C. J. Donoghue. 2017. Constraining the timing of whole genome duplication in plant evolutionary history. *Proceedings of the Royal Society B: Biological Sciences* 284:20170912.

Reports results from analyses to test the hypothesis, in a palaeobotanical context, that whole genome duplication leads to evolutionary innovation, increased diversity, and resistance to extinction. The inference that duplications happened in stem lineages fails to support the hypothesis but does corroborate the notion of a lag occurring between genome duplications and the origin of evolutionary diversification.

Estep, Matt C., Michael R. McKain, Dilys Vela Diaz, et al. 2014. Allopolyploidy, diversification, and the Miocene grassland expansion. *Proceedings of the National Academy of Sciences of the United States of America* 111.42: 15149–15154.

A phylogenomic investigation of whole genome duplications in grasses. The researchers identified more than thirty duplications within this clade alone, and time their origins to the Miocene when the grassland biome was expanding globally. This raises the possibility that these duplications may have laid the groundwork for evolutionary processes that helped establish these biomes.

Palmer, Jeffrey D., Douglas E. Soltis, and Mark W. Chase. 2004. The plant tree of life: An overview and some points of view. *American Journal of Botany* 91:1437–1445.

Provides a synopsis of the papers included in this special issue and highlights the questions that remain to be addressed, some of which persist into the 21st century. The included articles review seminal papers on cladistic analyses of plant morphological data and report results from the earliest molecular phylogenies and from the early phase of multilocus phylogenetic analyses.

Panchy, Nicholas, Melissa Lehti-Shiu, and Shin-Han Shiu. 2016. Evolution of gene duplication in plants. *Plant Physiology* 171:2294–2316.

A detailed review on the prevalence, mechanisms, and consequences of whole genome duplication in plants.

Puttick, Mark N., Jennifer L. Morris, Tom A. Williams, et al. 2018. The interrelationships of land plants and the nature of the ancestral embryophyte. *Current Biology* 28.5: 733–745.

A thorough analysis of phylogenomic datasets that finds support for the monophyly of liverworts + mosses (consistently) and a clade of liverworts and mosses + hornworts (less consistently). Both results suggest that the ancestral embryophyte was more complex than has been implied by phylogenies that suggest that liverworts are the sister group to all other land plants, and that the simpler morphology of liverworts resulted from character losses and transformations.

Sharborough, Joel, Justin L. Conover, Jennifer A. Tate, Jonathan F. Wendel, and David B. Sloan. 2017. Cytonuclear responses to genome doubling. *American Journal of Botany* 104:1277–1280.

An essay that highlights the importance of maintaining successful interactions between the genomes of the nucleus, plastid, and mitochondria following whole genome duplication of the nuclear genome. Outlines important research questions that should be addressed to understand how plants respond when cytonuclear interactions are perturbed by genome duplication.

Wickett, Norman J., Siavash Mirarab, Nam Nguyen, et al. 2014. Phylotranscriptomic analysis of the origin and early diversification of land plants. *Proceedings of the National Academy of Sciences of the United States of America* 111:E4859–E4868.

The most comprehensive phylogenomic inference of land plants to date, balancing taxon and gene sampling. It included ~90 taxa and nearly nine hundred gene regions derived from sequencing transcriptomes.

The Evolution of Plant Form

The ten living land plant clades, including those with the simplest forms (i.e., the bryophyte clades), are characterized by their morphological disparity or distinctness from one another. Evolutionary trajectories of disparity and diversity are decoupled in plants (Oyston, et al. 2016). For example, the basic, iconic morphology of ferns evolved early in their history, but their major diversification occurred much later. Similarly, the angiosperm flower marks the origin of angiosperms sometime between 135 and 200 MA, but the radiation of the largest clade (the eudicots) did not begin until about 125 MA, perhaps in association with the formation of symbioses with bee pollinators. The basic building blocks of plant form are shoots, branches, leaves, and roots. The position, arrangement, morphology, and growth patterns of these features (and in some cases their presence or absence) helps to generate the astonishing diversity we see in the 21st century. The study of traits associated with major evolutionary transitions from one form to another (such as from spore- to seed-bearing plants), and the subsequent radiations based on innovation within a particular form, has been transformed rapidly in recent years by the application of genetic and genomic approaches to identify the pathways that control these traits (Ambrose and Purugganan 2012; Bowman, et al. 2016; Graham, et al. 2000; Harrison 2017; Pires and Dolan 2012). Patterns of cell division and modifications in cell walls and cuticle are central to the development of diverse three-dimensional forms (Buschmann and Zachgo 2016, Monniaux and Hay 2016). A common macroevolutionary insight to emerge from these studies is that key traits are established by incremental changes occurring across multiple nodes in the green plant phylogeny (Catarino, et al. 2016). The data on traits that promoted disparity and diversity thus further strengthened the notion that the appearance of significant innovations does not happen at a single node in a phylogenetic tree but rather is distributed across a series of nodes (Donoghue 2005). Similarly, genome-scale data have demonstrated that gene families with roles in determining these traits are often conserved from algae to flowering plants but that their copy number may expand after an evolutionary transition. When duplicate gene copies are retained within a genome, subsequent divergence in their sequences might lead to the origin of a new function in one copy or subdivision between the two copies of functions previously combined in the single ancestral copy, potentially allowing greater scope for innovation in form and function.

Ambrose, Barbara A., and Michael D. Purugganan. eds. 2012. *The evolution of plant form*. Oxford: Blackwell Scientific.

This collection brings together chapters on morphological diversity and on the genetic mechanisms that might underpin this diversity.

Bowman, John L., Keiko Sakakibara, Chihiro Furumizu, and Tom Dierschke. 2016. Evolution in the cycles of life. *Annual Review of Genetics* 50:133–154.

Changes in life cycle as well as in form accompanied major evolutionary transitions. This is a broad review on the evolution of life cycles of land plants (and other multicellular organisms) with details on the genetic basis of life cycles in bryophytes and angiosperms.

Buschmann, Henrik, and Sabine Zachgo. 2016. The evolution of cell division: from streptophyte algae to land plants. *Trends in Plant Science* 21:872–883.

Reviews mechanistic details on cell division and discusses how specific changes during the evolution of cell division set the stage for the development of three-dimensional forms in land plants.

Catarino, Bruno, Alexander J. Hetherington, David M. Emms, Steve Kelly, and Liam Dolan. 2016. The stepwise increase in the number of transcription factor families in the Precambrian predated the diversification of plants on land. *Molecular Biology and Evolution* 33:2815–2819.

Reports results from a comparative analysis of families of transcriptome factors (TF) and their diversification during the evolution of plants, identifying families of plant TF that originated prior to colonization of land and their subsequent increase in size as plants diversified.

Donoghue, Michael J. 2005. Key innovations, convergence, and success: Macroevolutionary lessons from plant phylogeny. *Paleobiology* 31:77–93.

Provides an overview of land plant phylogeny and shows that the evolution of traits often thought to be key innovations that triggered increases in rates of diversification actually evolved in a stepwise manner over a series of nodes in the land plant phylogeny.

Graham, Linda E., Martha E. Cook, and James S. Busse. 2000. The origin of plants: Body plan changes contributing to a major evolutionary radiation. *Proceedings of the National Academy of Sciences, USA* 97.9: 4535–4540.

A wide-ranging review covering the origin and innovations in plant body plans, including an overview of the genes that might have played key roles in morphological transitions.

Harrison, C. Jill. 2017. Development and genetics in the evolution of land plant body plans. *Philosophical Transactions of the Royal Society of London. Series B* 372:20150490.

A broad synthetic perspective on the origin, phylogenetic distribution, and emerging perspectives on the genetic basis of key traits.

Monniaux, Marie, and Angela Hay. 2016. Cells, walls, and endless forms. *Current Opinion in Plant Biology* 34:114–121.

Discusses the cellular basis of diversity in plant form, highlighting the roles of modifications to cell walls and cuticles.

Oyston, Jack W., Martin Hughes, Sylvain Gerber, and Matthew A. Wills. 2016. Why should we investigate the morphological diversity of plant clades? *Annals of Botany* 117:859–879.

Discusses the importance of distinguishing between disparity and diversity and shows that most major clades of plants demonstrate initial high levels of disparity before diversifying as they explore the morphospace associated with specific body plans.

Pires, Nuno D., and Liam Dolan. 2012. Morphological evolution in land plants: New designs with old genes. *Philosophical Transactions of the Royal Society of London. Series B* 367:508–518.

An overview of land plant evolution with a focus on genes and developmental mechanisms involved in generating diversity.

Temporal Patterns of Land Plant Diversification

The stratigraphic appearance of land plants in the fossil record establishes a timeline for their origin and for dating the origins of important innovations such as vasculature, wood, roots, and leaves (Kenrick, et al. 2012). The fossil record has numerous gaps, however, and it is now common practice to infer a timeline for the origin of the living lineages by integrating fossil evidence with molecular phylogenetic analyses, where fossils are used to constrain the window of time during which a split in the molecular phylogeny occurred. Studies using Bayesian and likelihood approaches use probabilities with maximum and minimum ages to model age estimates. Accurate ages of land plants are critical for calibrating coincident events in biome, animal, fungal, or biogeochemical evolution, yet the age estimates of most early-diverging land plants have not reached a broad consensus. This is partly attributable to the dearth of early plant fossils but also to a potentially significant lag period between the origin of lineages and the first appearance of features that allow us to definitively place these fossils. The scarcity of lineages arising during the lag period may further confound age estimation, since there will be limited fossil evidence to represent them. The most recent age estimates drawn from genomic data and over a dozen fossil constraints suggest that crown group land plants originated anywhere between 816–568 MYR (Clarke, et al. 2011; Morris, et al. 2018). The older estimates, however, are far out of alignment with the geological record. Estimates for vascular plants (Tracheophyta) are from 456–425 MYR and for seed plants (Spermatophyta) from 368–330 MYR. Angiosperms are the primary producers and most conspicuous structural elements of our modern terrestrial ecosystems, and their age remains especially contentious (Beaulieu, et al. 2015; Magallón, et al. 2015). One challenge here is the long, empty branch that separates crown group angiosperms from their closest living gymnosperm relatives in molecular phylogenies. Another is that the position of fossil gymnosperm lineages in seed plant phylogenies remains uncertain. The fossil record indicates that angiosperms diversified in the Early Cretaceous (~135 MYR), consistent with recent ages estimated for crown group angiosperms in the Early Cretaceous; Monocots and Eudicots diversified at 135–130 MYR; Rosidae at 123–115 MYR; and Asteridae at 119–100 MYR. The age of angiosperms has been more difficult to pinpoint, as previously noted, due to the scarcity of fossil evidence before their major radiation. Most estimates from molecular dating place their origin in the Jurassic (200–145 MYR). The importance of the role of extinction to our understanding of temporal patterns of land plant evolution is highlighted by Knoll 1984, Crisp and Cook 2011, and Laenen, et al. 2014.

Clarke, John T., Rachel C. M. Warnock, and Philip C. J. Donoghue. 2011. Establishing a time-scale for plant evolution. *New Phytologist* 192:266–301.

A thoughtful attempt to synthesize seventeen well-placed fossils, of minimum and maximum ages, with molecular divergence time estimates. Provides a chronology of all major land plant clades including an age of crown group land plants (embryophytes) of 815–568 MYR and crown group angiosperms of 250–175 MYR.

Beaulieu, Jeremy M., Brian C. O'Meara, Peter R. Crane, and Michael J. Donoghue. 2015. Heterogeneous rates of molecular evolution and diversification could explain the Triassic age estimate for angiosperms. *Systematic Biology* 64:869–878.

This study calls into question the Triassic age of crown group angiosperms commonly identified in molecular clock investigations in which the crown group angiosperm node is unconstrained. This age is much older than the commonly accepted age of ~135 MA based on direct fossil evidence. Major differences in sequence evolution among early clades of angiosperms and taxon sampling were identified as contributors to the elevated ages of these groups.

Clarke, John T., Rachel C. M. Warnock, and Philip C. J. Donoghue. 2011. Establishing a time-scale for plant evolution. *New Phytologist* 192:266–301.

A thoughtful attempt to synthesize seventeen well-placed fossils, of minimum and maximum ages, with molecular divergence time estimates. Provides a chronology of all major land plant clades including an age of crown group land plants (embryophytes) of 815–568 MYR and crown group angiosperms of 250–175 MYR.

Crisp, Michael D., and Lyn G. Cook. 2011. Cenozoic extinctions account for the low diversity of extant gymnosperms compared with angiosperms. *New Phytologist*. 192:997–1009.

Despite the extraordinarily recent radiation of angiosperms, long thought to be unique to this clade, recent evidence suggests that three of the other seed plant clades (cycads, conifers, and gnetophytes) show rates of speciation that are comparable to angiosperms. The disparity between angiosperm and gymnosperm diversity results in part from high extinction in the Mesozoic.

Kenrick, Paul, Charles H. Wellman, Harald Schneider, and Gregory D. Edgecombe. 2012. A timeline for terrestrialization: Consequences for the carbon cycle in the Palaeozoic. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 367:519–536.

An in-depth exploration comparing fossils with molecular phylogenetic trees, including for plants and arthropods. A beautiful depiction of the dated origins of key land plant features, including cuticle, tracheids, roots, and arborescence. There are a number of key conflicts identified between these two data sources. The paper calls for more time trees better constrained by fossils and a more critical assessment of the fossil and sedimentary record.

Knoll, Andrew H. 1984. Extinction of vascular plants. In *Extinctions*. Edited by Matthew H. Nitecki, 21–68. Chicago: Univ. of Chicago Press.

A seminal analysis of extinction patterns in vascular plants, demonstrating the importance of competition from newly evolved and diversifying lineages over climate change in structuring macroevolutionary patterns of vascular plant diversity through time, and showing that mass extinctions had relatively little impact.

Laenen, Benjamin B. Shaw, Harald Schneider, Bernard Goffinet, et al. 2014. Extant diversity of bryophytes emerged from successive post-Mesozoic diversification bursts. *Nature Communications* 5134: 1–6.

Bryophytes are substantially less diverse than ferns and angiosperms, but this study presents evidence of bursts of diversification of both liverworts and mosses and suggests that low species richness in living bryophytes results partly from massive extinctions.

Magallón, Susana, Sandra Gómez-Acevedo, Luna L. Sánchez-Reyes, and Tania Hernández-Hernández. 2015. A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytologist* 207:437–453.

The most comprehensive assessment to date estimating the origin and diversification of major flowering plant clades. The study samples nearly 90 percent of angiosperm families and applied an impressive 137 fossil calibrations. Their results suggest that the broad outline of angiosperm diversity—over half of the extant families—arose long ago in the Cretaceous but that most extant species diversity arose later.

Morris, Jennifer L., Mark N. Puttick, James W. Clark, et al. 2018. The timescale of early land plant evolution. *Proceedings of the National Academy of Sciences, USA*.

A thorough analysis to establish a timescale for early land plant evolution that estimates a Middle Cambrian to Early Ordovician origin of land plants, coinciding with the origin of terrestrial animal lineages.

Global Impacts of Land Plants

Land plants have transformed our planet. Their biological activities have had dramatic effects on the atmosphere, the radiative environment of the earth's surface, and the origin, composition, and chemistry of soils. These impacts established environments for the origin and diversification of other organisms. Vegetation and the microflora of algae and bryophytes have had a significant, long-term impact on the global carbon and nitrogen cycles (Elbert, et al. 2012; Lenton, et al. 2012; Knack, et al. 2015), and the major decrease in carbon inferred to have occurred around 380–350 MA is attributed to the advent of trees. Vegetation also alters climate (Boyce and Lee 2017). It does so by its impacts on the proportion of solar energy that is reflected rather than absorbed (the albedo), the degree of surface roughness (which influences wind speed and turbulence), transpiration (i.e., the movement of water through the plant and its diffusion to the atmosphere), and evaporation. The impact of plants on other organisms is no less significant. Herbivores of all sizes, from microscopic invertebrates to large dinosaurs, have relied on the trophic foundation of land plants. The eudicots, which include ~75 percent of all angiosperms underwent coincident diversification with their primary pollinators, bees, around 125 MYR (Cardinal and Danforth 2013). And numerous groups, including ferns (Schuettpezel and Pryer 2009), orchids, and ants appear to have diversified in angiosperm canopies, which developed especially during the Cenozoic (within the last 65 MYR). One remarkable example within angiosperms

involves the expansion of North American grasslands and parallel diversification events within two equid lineages (horses and their relatives). Grasslands expanded in the Miocene and Pliocene in response to climatic and geological factors and now occupy 20–40 percent of the earth's surface. Diversification within grasslands, particularly the rise of C₄ grasses, was further influenced by climatic factors including decreases in atmospheric CO₂ and mean annual precipitation, along with increases in fire frequency. And this was also associated with the diversification of equids and the evolution of dental adaptations to diets higher in grit, ingested with soil and/or as grass phytoliths (Damuth and Janis 2011; McInerney, et al. 2011). The sources in this section highlight the abiotic and biotic factors influenced by land plant evolution, especially the origin of the angiosperms.

Boyce, C. Kevin, and Jung-Eun Lee. 2017. Plant evolution and climate over geological timescales. *Annual Review of Earth and Planetary Sciences* 45:61–87.

A broad review on the evolution of floral composition, plant physiology, and the seasonal and spatial landscape of land plants in the context of how vegetation altered climate through time. Focuses mostly on the climatic variables, temperature, and precipitation, showing that the greatest feedbacks are likely to have been experienced during the Carboniferous and Early Paleogene.

Cardinal, Sophie, and Bryan N. Danforth. 2013. Bees diversified in the age of eudicots. *Proceedings of the Royal Society B: Biological Sciences* 280:20122686.

Molecular divergence dates for a broad sample of bees to determine the timeline for bee diversification, the primary pollinators of angiosperms. Their relaxed clock models indicate that crown group bees originated ~125 MYR coincident with the origin of the largest clade of angiosperms: the eudicots. Similarly, all major lineages of bees were estimated to have originated in the Middle to Late Cretaceous when most major angiosperm lineages became dominant.

Damuth, John, and Christine M. Janis. 2011. On the relationship between hypsodonty and feeding ecology in ungulate mammals and its utility in palaeoecology. *Biological Reviews* 86:733–758.

A detailed review of the relationship between hypsodonty (having high-crowned teeth) and the ecology of ungulates. Asserts that hypsodonty is relevant to understanding feeding behavior and that incorporating evidence for the consumption of soil by ungulates feeding on grasses improves our understanding of the correlation between diets, habitats, and hypsodonty.

Elbert, Wolfgang, Bettina Weber, Susannah Burrows, et al. 2012. Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nature Geoscience* 5:459–462.

Focuses on the contribution by cryptogamic covers of terrestrial surfaces, components of which include algae and bryophytes, to global and regional cycling of carbon and nitrogen. Estimates that they are responsible for nearly half of the biological fixation of nitrogen on land, suggesting this is critical for carbon sequestration by plants.

Knack, Jennifer J., Lee. W. Wilcox, Pierre-Marc Delaux, et al. 2015. Microbiomes of streptophyte algae and bryophytes suggest that a functional suite of microbiota fostered plant colonisation of land. *International Journal of Plant Sciences* 176:405–420.

Presents findings from a metagenomics study indicating that modern streptophyte algae and bryophytes are associated with a diverse array of microbes that suggest early land plants likely had a significant impact on global nitrogen and carbon cycling.

Lenton, Timothy M., Michael Crouch, Martin Johnson, Nuno Pires, and Liam Dolan. 2012. First plants cooled the Ordovician. *Nature Geoscience* 5:86–89.

Combines weathering experiments with a model-based approach to predict the effects of weathering on plant colonization in an attempt to understand the contribution of colonization to global changes in levels of atmospheric CO₂.

McInerney, Francesca A., Caroline A. E. Strömberg, and James W. C. White. 2011. The Neogene transition from C₃ to C₄ grasslands in North America: Stable carbon isotope ratios of fossil phytoliths. *Paleobiology* 37:23–49.

Presents results from careful analyses of carbon isotope ratios for fossil assemblages of plant silica bodies that demonstrate changes in grass communities during the Late Miocene and Pliocene. A transition from communities of predominantly C₃ grasses to mixed C₃-C₄ grasses had occurred by 5.5 MA and was followed by a shift to 80 percent C₄ grasses by 3–2 MA.

Schuettpelz, E., and K. M. Pryer. 2009. Evidence for a Cenozoic radiation of ferns in an angiosperm-dominated canopy. *Proceedings of the National Academy of Sciences of the United States of America* 106:11200–11205.

This study inferred a dated phylogeny of ferns demonstrating that numerous epiphytic radiations occurred just after the K-T boundary (65 Myr) during which time forests became dominated by large angiosperm trees. These angiosperm canopies were thought to have provided a novel environment for ferns that enhanced their diversification.

Emerging Insights, Challenges, and Future Prospects

A major remaining challenge to understanding land plant evolution stems from the limited ability to integrate fossil and molecular data to increase the accuracy and power of phylogenetic inference for assessing land plant diversification. Extinction has had a significant impact throughout their history, for example, trimming up to 70 percent of the major lineages of seed-bearing plants. Their absence from most phylogenetic studies, along with the absence of extinct non-seed-bearing plants, greatly compromises the accuracy of inferred phylogenies and restricts our ability to effectively date and describe the plant tree of life. This challenge is exacerbated by the small number of morphological characters that can be assessed for inclusion in analyses, even when fossils are available, thus reducing their impact, particularly when combined with vast amounts of genomic data. To meet the challenge, new advances are enabling the integration of dense fossil records into hierarchical phylogenetic models to assess major patterns of lineage origination and extinction (Silvestro, et al. 2015). Additionally, the use of emerging imaging technologies is expanding the amount and detail of data to be gleaned from newly discovered and existing fossils. Along these lines, X-ray synchrotron microtomography is a promising direction for nondestructively reconstructing the soft tissues of fossil and modern plants as three-dimensional models (Smith, et al. 2009). And in our era of rapidly increasing specimen data mobilized online via digitization, machine learning algorithms offer tremendous promise for harvesting new sources of phenotypic data for evolutionary investigations. Pipelines for automated capture and processing of data on gross morphology from digital images of specimens are being developed to meet the challenge of making it as easy to capture phenotypic data as it is to capture genomic data (Wilf, et al. 2016). These next generation phenotypic methods offer promising new interfaces with comparative genomics (Bowman, et al. 2017) to reveal the genetic and genomic basis of traits that characterize the milestones of land plant evolution.

Bowman, John L., Takayuki Kohchi, Katsuyuki T. Yamato, et al., and Jeremy Schmutz. 2017. Insights into land plant evolution garnered from the *Marchantia polymorpha* genome. *Cell* 171:287–304.

A comprehensive comparative genomics assessment on the patterns of gene acquisition and loss involved in transcription, signaling, and biochemistry during the origins of land plants from their closest algal relatives.

Sauquet, Hervé, Maria von Balthazar, Susana Magallón, et al. 2017. The ancestral flower of angiosperms and its early diversification. *Nature Communications* 8:16047.

A phylogenetic assessment of the ancestral flower, which suggests the ancestral flower was bisexual and radially symmetrical, with multiple whorls of undifferentiated perianth and stamens and spirally arranged carpels. This contradicts common wisdom that the ancestral flower was not composed of spirally arranged parts, indicating that more recently evolved angiosperms achieved their canonical configuration (two perianth whorls and two staminal whorls) as a result of reduction.

Silvestro, Daniele, Borja Cascales-Miñana, Christine Bacon, and Alexandre Antonelli. 2015. Revisiting the origin and diversification of vascular plants through a comprehensive Bayesian analysis of the fossil record. *New Phytologist* 207:425–436.

By applying a novel Bayesian analysis of plant localities and hundreds of macrofossils, the article assesses the Big Five mass extinctions to determine lineage origination and extinction. Their results corroborate major episodes of floral turnover during some of these events, including high origination rates occurring at the Middle Devonian, the Early Triassic, and the Early Paleogene. The highest extinction rates take place at the Paleozoic-Mesozoic boundary and during the Late Devonian.

Smith, Selena Y., Margaret E. Collinson, Paula J. Rudall, David A. Simpson, Federica Marone, and Marco Stampanomi. 2009. Virtual taphonomy using synchrotron tomographic microscopy reveals cryptic features and internal structure of modern and fossil plants. *Proceedings of the National Academy, USA* 106:12013–12018.

Describes the use of X-ray tomographic microscopy and demonstrates its utility for revealing cryptic features in both modern and fossil plants.

Wilf, Peter, Shengping Zhang, Sharat Chikkerur, Stefan A. Little, Scott L. Wing, and Thomas Serre. 2016. Computer vision cracks the leaf code. *Proceedings of the National Academy of Sciences* 113:3305–3310.

Develops a machine learning approach to facilitate plant identification from cleared and stained leaf samples. Specimens were identified to family and order with high reliability. Moreover, key traits identified for groups often departed from those traditionally used by humans, suggesting novel sources of important functional traits that have been overlooked.

[back to top](#)